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NATURAL HYBRIDIZATION BETWEEN CUCURBITA DIGITATA AND C. PALMATA

W. P. Bemis and Thomas W. Whitaker

Cucurbita digitata Gray and *C. palmata* Wats. are xerophytic, perennial species indigenous to the desert regions of southwestern United States and northwestern Mexico.[1] According to Bailey (1943) *C. digitata* is found in New Mexico, Arizona, sparingly in southeastern southern California (eastern Riverside County) and in Sonora, Mexico. It is doubtful that *C. digitata* is indigenous west of the Colorado River. In California it is found in limited roadside areas, suggesting that it was probably introduced by camper-tourists. *Cucurbita palmata* is found in southern California from the Mohave Desert southwards in interior valleys and at low elevations. It also occurs in western Arizona and northern Baja California, Mexico. In the area adjacent to the Arizona-California border and directly east of the Colorado River the species are sympatric.

Each species has 20 pairs of chromosomes (McKay, 1931). They also have similar growth patterns. The root systems have large fleshy storage roots which enable the plants to survive prolonged periods of high temperatures and extremely arid conditions. Vine growth is rapid under favorable conditions of moisture and temperature. Adventitious roots are produced at intervals on the nodes of the runners, and under favorable moisture conditions these roots are able to develop into tuberous roots which when separated from the mother vine will establish another plant. This asexual method of propagation produces a clone with the individual plants grouped in colonies. *Cucurbita digitata* and *C. palmata* are prolific producers of fruit and seed. The fruit is a relatively hard-shelled, round pepo, two to three inches in diameter, and contains from 200 to 600 seeds. Reproduction by seed, however, is probably limited because of low seed and seedling survival in the environments to which these species are adapted.

[1] We wish to acknowledge with thanks the assistance of F. D. Cole, University of Arizona, and Paul D. Hurd, Jr., University of California, Berkeley, for directing our attention to localities where hybrids were likely to occur. Dr. Hurd and Dr. Edgar Anderson have read and made suggestions for improvement of the manuscript.

Methods and Results

The most conspicuous morphological difference between the two species is leaf shape. The leaf of *C. digitata* has five lanceolate lobes with sinuses developed to the base of the leaf veins. The leaf of *C. palmata* has five palmate lobes with sinuses developed to approximately one-third the length of the leaf veins. The first four to six seedling leaves of both species are similar to *C. palmata*.

Since leaf shape is the most striking morphological difference between these species a method of measurement was developed to describe the leaves numerically. The measurement that was found to reflect the leaf diffrences was the ratio of the length to the width of the central palmate or lanceolate lobe and the two adjacent lobes. The length of the lobes was measured from the petiole attachment to the tip of the leaf blade. The widths of the lobes were measured at their widest point not including appendages which were present on some leaves. The widest point on the lobes of *C. palmata* leaves was at the base of the sinuses.

Figure 1 shows three diagrammatic *Cucurbita* leaves superimposed. The solid leaf represents *C. digitata* and has a length to width ratio of ten. The open leaf represents *C. palmata,* with a length to width ratio of two. The shaded leaf is intermediate between *C. digitata* and *C. palmata* with a length to width ratio of five and represents an F_1 hybrid between the two species.

Greenhouse Observations. As a part of a general study of the genus *Cucurbita,* reciprocal crosses between *C. digitata* and *C. palmata* were made. The F_1 and F_2 generations were fertile, indicating these species are cross compatible.

Plants from self-pollinated seed of two *C. digitata* lines and one *C. palmata* line, along with the reciprocal F_1 hybrids were grown in the greenhouse at the University of Arizona in the fall of 1963. The *C. digitata* lines originated from fleshy roots collected 5 miles and 22 miles N of Tucson, Arizona. The *C. palmata* line came from a fleshy root collected in the Yuma Valley, Arizona, adjacent to the Colorado River and 5 miles N of the Mexican border. Leaf ratio measurements for these seven plants are given in Table 1. Leaf ratios for the two *C. digitata* lines were 9.42 ± 1.66 and $8.34 \pm .72$ respectively, while for *C. palmata* the ratio was $2.28 \pm .27$. For the F_1 hybrids of *C. digitata* ♀ x *C. palmata* ♂ the leaf ratio were $4.62 \pm .39$ and $4.89 \pm .39$; for the reciprocal cross the ratios were $3.87 \pm .79$ and $3.65 \pm .73$ (fig. 2). It is evident that the F_1 hybrids are intermediate between the parent species. Data from the hybrids suggest a possible cytoplasmic effect on leaf ratios as they tend to show an effect of the female parent. More information on this question is necessary before a statement can be made. The point is that both kinds of hybrids do have intermediate leaf ratios.

Field Observations. The range of *C. digitata* and *C. palmata* overlap in the vicinity of the Arizona-California border roughly parallel to the Colorado River from near the vicinity of Davis Dam in southern

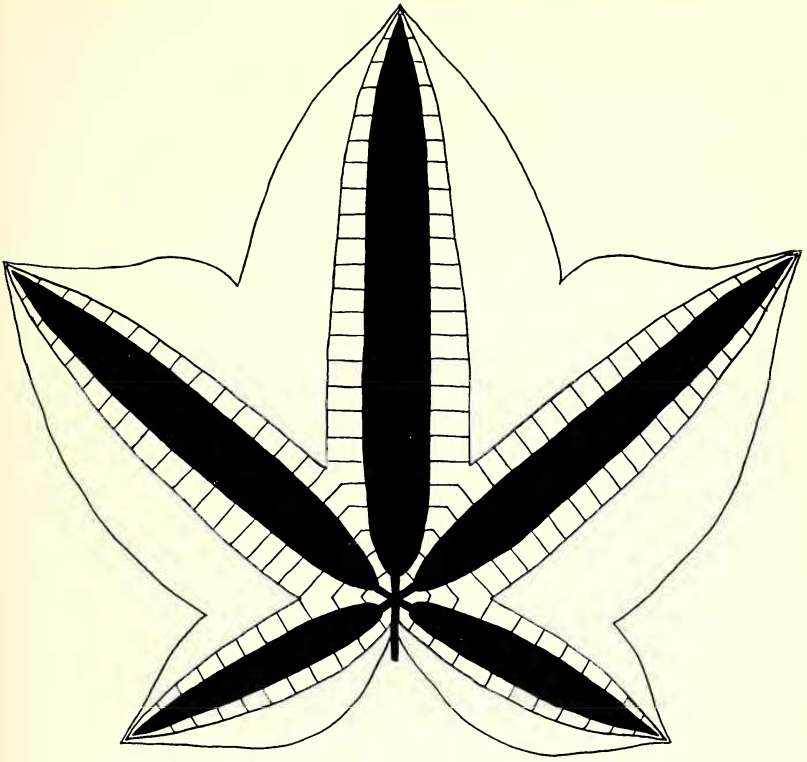

FIG. 1. Diagrammatic sketch representing a leaf of *C. digitata* (solid), *C. palmata* (open), and an intermediate (shaded).

Nevada, on the north to San Luis, Sonora, Mexico, on the south. In this general area one might expect natural hybridization between the two species to occur. Our attention was directed to some plants which appeared to be suspiciously like hybrids in the area north of Dateland, Arizona, by F. D. Cole and to the area between Quartzite, Arizona, and Yuma, Arizona paralleling Arizona Highway 95 by P. D. Hurd, Jr. Collections were made in the above two areas, and in a third area where Highway 95 crosses the Gila River, about 12 miles NW of Yuma and 6 miles E of the Colorado River. At each location herbarium specimens (ARIZ) were collected and leaf ratios were obtained.

Dateland locality. This locality is in the bed of the Gila River north of Dateland, Arizona. It is approximately 70 miles E of the Colorado River (Arizona-California border). The Gila River at this point forms a flood plain about two miles wide. The soil of the plain is a silty loam and it supports a dense growth of mesquite. The samples were taken from the south edge of this flood plain on Nov. 21, 1963. The soil of the flood plain had at one time been disturbed by heavy equipment operating at

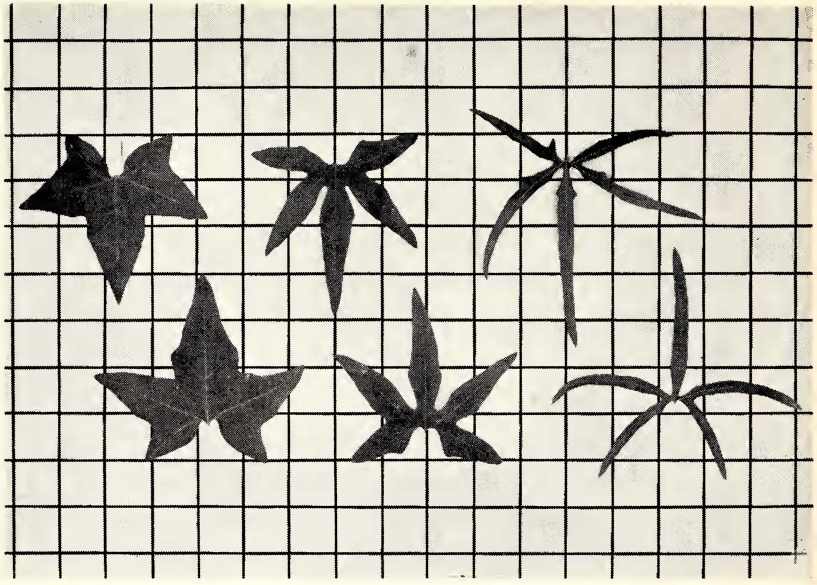

FIG. 2. Two representative leaves of *C. palmata* (left); F_1 (*C. palmata* × *C. digitata*) center; and *C. digitata* (right). Hybrids were produced from controlled pollinations.

a nearby sand and gravel quarry. The action of this equipment may have created favorable conditions for seed germination and seedling establishment of *Cucurbita* seed produced locally or from fruit transported down the Gila River during periods of flooding.

A particularly dense population of *Cucurbita* occupied an area approximately 90 × 150 feet (fig. 3). From this area fourteen individual colonies were sampled. The leaf ratio data are given in Table 1 under "Dateland." Two plants from this area had leaf ratios indicative of "pure" *C. digitata,* and one plant was identified as *C. palmata* based on leaf ratio data. The remaining eleven plants had intermediate leaf ratios varying from 5.60 ± .72 to 2.97 ± .38 (fig. 4). The range in leaf ratios of intermediates suggests that they include segregates beyond the F_1 generation or perhaps backcrosses, or if they are representative of F_1 hybrids, that the parental species were not homozygous for factors controlling leaf shape. Plants with intermediate leaf ratios are undoubtedly the result of natural interspecific hybridization.

Yuma locality. A sample was taken where U.S. Highway 95 crosses the Gila River. This area is approximately 6 miles E of the Colorado River and 64 miles down river from the Dateland sampling area. The *Cucurbita* at this location were not particularly dense and only seven colonies were sampled on Dec. 19, 1963, in approximately a quarter mile length of the Gila River. Leaf ratio data for the seven plants from this area are given in Table 1 under "Yuma."

FIG. 3. Field photograph from Dateland, Arizona, showing runners from plants with digitata-like and palmata-like colonies intertwined. The pole is marked in dms.

Three of the plants had leaf ratios indicative of *C. palmata*, a fourth was like *C. palmata* but showed some indication of *C. digitata* contamination since it had a leaf ratio of 2.85 ± .27. Two plants were intermediate, and one plant was principally *C. digitata* but showed some evidence of *C. palmata* contamination with a leaf ratio of 7.14 ± .87. These limited data suggest that the dominant species in this area is *C. palmata* and that fruit and seed of *C. digitata* segregates were probably transported down the Gila River during periods of flooding.

Five locations on Highway 95. Eighteen colonies were sampled on Dec. 3, 1963, at 5 locations extending from 18 to 55 miles S of Quartzite, Arizona, on Highway 95. The colonies were located either in the stream bed or along the banks of dry washes that drain westward into the Colorado River. Abundant late summer and fall rains had produced excellent vegetative growth, but flowers and fruits were absent from most colonies.

Of the 18 colonies sampled, one appeared to be "pure" *C. palmata*, and 5 were *C. digitata* or *digitata*-like (Table 1). The remainder were inter-

TABLE 1. LEAF LENGTH/WIDTH RATIOS OF LEAVES OF CUCURBITA DIGITATA, C. PALMATA AND HYBRIDS FROM GREENHOUSE PLANTS AND FROM PLANTS SAMPLED AT VARIOUS FIELD LOCATIONS. THE LEAF MEASUREMENTS ARE THE AVERAGE OF 5 MATURE LEAVES FROM EACH COLONY

				Five Locations on U.S. Highway 95				
		Dateland	Yuma	18 colonies				
	Greenhouse	14 colonies	7 colonies	1	2	3	4	5
				digitata-like				
C. digitata #1	9.42 ± 1.66	11.29 ± 2.15						
C. digitata #2	8.34 ± .72	8.64 ± 1.03						
			7.14 ± .87		7.30 ± .82	7.41 ± 1.59	7.56 ± 1.62	
								6.95 ± .25
				intermediate				
						6.29 ± 1.04		
				6.25 ± .38		6.25 ± .70		6.28 ± .73
						5.62 ± .81		
		5.60 ± .72					5.35 ± .40	
		5.07 ± .50						
F_1 (*dig.* × *pal.*)	4.83 ± .39	4.76 ± .65	4.80 ± .87	4.82 ± .37				
	4.62 ± .39	4.58 ± .51		4.80 ± .87		4.87 ± .93		
		4.32 ± .31	4.27 ± .27					
		4.22 ± .59						
F_1 (*pal.* × *dig.*)	3.87 ± .79	3.48 ± .35		3.96 ± .29		3.58± .92		
	3.65 ± .73	3.56 ± .44			3.43 ± .20			
		3.33 ± .39			3.41 ± .45			
		3.09 ± .60						
		2.97 ± .38	2.85 ± .27					
				palmata-like				
C. palmata	2.28 ± .27	2.19 ± .28	2.31 ± .15					2.10 ± .31
			2.17 ± .19					
			2.09 ± .15					

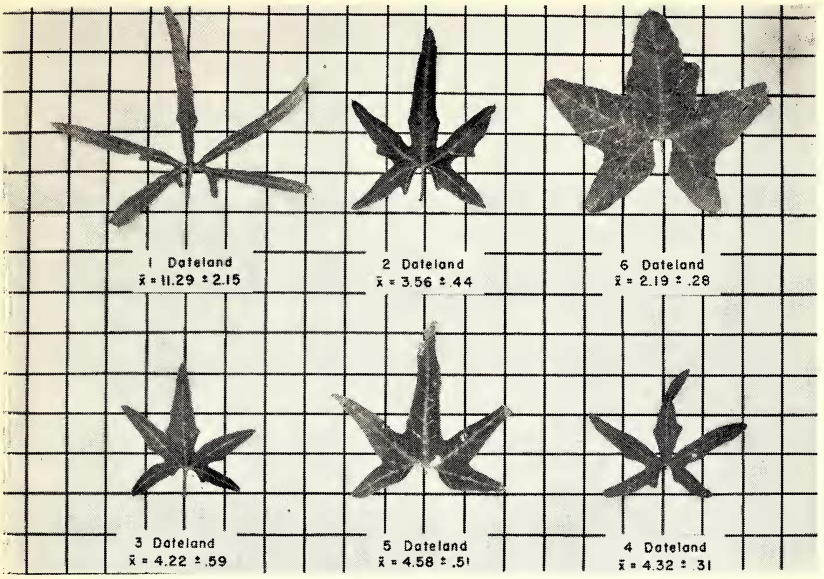

FIG. 4. Leaves from natural hybrids, Dateland; 1 (upper left) is "pure" digitata; 6 (upper right) is "pure" palmata; the remainder, 2–5, are intermediates.

mediates, but a majority of these plants were more like *C. digitata* than *C. palmata*. There was no noticeable trend in favor of one or another of the two species from north to south, nor did the individual sampling areas appear to be homogeneous for leaf type.

DISCUSSION

Two perennial, xerophytic species of *Cucurbita, C. digitata* and *C. palmata,* were successfully hybridized under controlled conditions. They produced fertile F_1 and F_2 progenies, indicating a marked degree of compatibility. Reasoning from this information, it was considered probable that natural hybridization might occur in locations where the ranges of the two species overlap. The area immediately east of the Colorado River, adjacent to the Arizona-California border and stretching north to south for a distance of 200 miles seems the most likely place for hybridization to occur. Before the search for natural hybrids could be profitably pursued, it was necessary to have a reliable morphological marker to indicate putative hybrids. The two species are nearly similar in vegetative, fruit and seed morphology, but there is a striking difference in one vegetative character, *leaf shape*. A ratio of the lobe length to lobe width was devised to describe numerically the leaves of the parent species and the hybrid between them.

Since these species are cross compatible and monoecious, we would anticipate considerable hybridization in nature if a suitable pollinator

were present. That such a pollinator is present was established by Hurd and Linsley (1964) in their scholarly studies of the squash and gourd bee of the genera *Xenoglossa* and *Peponapis*. The authors report that one species, *P. timberlakei*, is limited to *C. digitata* and *C. palmata* for its pollen and nectar supplies. Apparently *P. timberlakei* cannot use the pollen of other *Cucurbita* species even when available within its range. The infrequent, but severe rainstorms that cause flooding and erosion in this area could produce niches free from competition where young *Cucurbita* seedlings would have an excellent chance to become established. Thus four elements for successful natural hybridization are present: 1, compatible species; 2, overlapping ranges; 3, an efficient pollinator; and 4, a niche for the survival of the hybrids.

Using the leaf ratio index as a criterion it is apparent from field collections that natural hybridization exists along a narrow front roughly parallel to the Colorado River in western Arizona. We are suggesting the two species migrated into the area and subsequently hybridized. This area of the Colorado River basin is traversed by the Gila River and numerous dry washes all flowing westward toward the Colorado River. Violent summer and fall rains, although relatively infrequent, produce much flooding and erosion and would be capable of transporting fruits and seeds from south and east central Arizona toward the Colorado.

Summary

1. F_1 and F_2 hybrid populations of *C. digitata* × *C. palmata* were produced in the greenhouse. These hybrids were fertile, indicating the two species are compatible.

2. *Cucurbita digitata* and *C. palmata* are sympatric along a narrow front parallel to and directly east of the Colorado River, extending from the vicinity of Davis Dam in southern Nevada to San Luis in northern Sonora, Mexico.

3. The most conspicuous morphological difference between the two species is the structure of the leaf. *Cucurbita digitata* has five lanceolate lobes with the sinuses extending to the base of the leaf. *Cucurbita palmata* has five palmate lobes with sinuses extending about one-third the distance to the base. A ratio was devised to reflect this difference: thus *C. digitata* has a length width ratio of 10; *C. palmata*—2; and the F_1 hybrid—5.

4. In the areas where the two species are sympatric we have sampled colonies in three locations and determined by leaf length to width ratios that natural hybridization has occurred.

5. We have shown that the elements for successful natural hybridization are present, i.e. compatible species, overlapping ranges, a specific pollinating insect, and niches for the survival of the hybrid seedlings.

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MANZANITA CHAPARRAL IN THE SANTA ANA MOUNTAINS, CALIFORNIA

R. C. Wilson and R. J. Vogl

A quantitative study of *Arctostaphylos glandulosa* Eastw. chaparral associations in the Santa Ana Mountains was undertaken during the years 1962 and 1963. This phytosociological study correlates numerical data with information on climate, soils, slope exposure, and elevation to estimate the stability, site preferences, and species associations for *Arctostaphylos glandulosa*.

Little consideration has been given to the quantitative aspects of chaparral associations dominated by *Arctostaphylos* species. Major attention has been given to *Adenostoma fasciculatum* H. & A. chaparral, a more widespread and lower elevation community. Extensive studies of *Arctostaphylos* chaparral have possibly been neglected because it is more restricted than *Adenostoma* chaparral, occurs at higher elevations which are often more difficult to reach, and is usually considered impenetrable. Since *Arctostaphylos* chaparral generally occurs at higher elevations, it does not present as many erosion, watershed, or fire problems and is considered of less economic, agricultural, or wildlife importance than chaparral types bordering grazing land, cultivation, or settlement.

The classic work of Cooper (1922) in central California is a floristic study of California chaparral (Delting, 1961). Cooper observed and commented on slope, exposure preferences, behavioral characteristics, humus accumulation, and evaporation ratios of *Arctostaphylos* associations as compared with other chaparral associations. Cooper cited 19 species of *Arctostaphylos* as components of chaparral and classified *Arctostaphylos* site requirements as intermediate between *Adenostoma fasciculatum* and coniferous forest.

Following Cooper's work, a number of studies were made of chaparral ecology, again mainly in *Adenostoma* communities. These include reports by Bauer (1936), Miller (1944; 1947), Sampson (1944), and Wells (1962). Sampson quantitatively studied chaparral succession in central and northern California. He indicated that pine suffered when associated with *Arctostaphylos* due to the greater potential of *Arctostaphylos* to recover after fire by resprouting or by seed germination. Some *Arcto-*